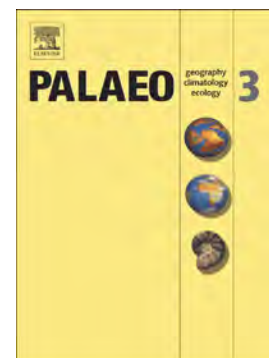


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Dietary response of early Pleistocene ungulate communities to the climate oscillations of the Gelasian/Calabrian transition in Central Italy

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Abstract

Climatic oscillations at the Gelasian/Calabrian transition modified terrestrial palaeoenvironmental settings in the European region. A gradual drop in global temperatures beginning about 2.7 Ma led to drier conditions and to a reduction in, and subsequent disappearance of, sub-tropical vegetation in the central Mediterranean area by ca 1.2 Ma. Large ungulates are sensitive to vegetation changes and faced with harsher environmental settings may shift their feeding strategies to exploit available food resources in different ecosystems. In fossil assemblages such dietary adaptations are reflected by tooth morphology (a phylogenetic signal) and tooth wear degree (a direct signal of the species' diet). In this paper, we investigate how large herbivores responded to palaeoenvironmental changes that occurred at the passage between the Gelasian and Calabrian ages in the Italian Peninsula, analysing the dental wear patterns and hypsodonty of the early Pleistocene fossil ungulates assemblage of Olivola (Aulla, Central Italy). We found that while

ungulate feeding behaviours during the Calabrian spanned from browsers to grazers, in the Gelasian locality of Olivola this group of herbivores display a narrower range of diet types with many taxa adopting a mixed feeding behaviour. Cervids in particular, whose fossils are often associated only with wooded environments, as a response to the reduction of covered sub-tropical vegetation, shifted from a strict browsing diet in mostly closed habitats to a more abrasive one taking advantage of the spread of open landscapes. We also provide new data on the feeding behaviour of the rare fossil caprines, *Procamptoceras* and *Gallogoral meneghinii*, suggesting a grass-rich mixed diet for the former and a certain degree of dietary plasticity for the latter. Our research thus contributes to the better understanding of how ungulates adapted in the past to exploit different resource types during pivotal climatic changes and how environments changed in Central Italy on the onset of colder and more arid conditions.

Keywords: Palaeoecology; Mesowear; Artiodactyls; Perissodactyls; Villafranchian.

1. Introduction

A gradual drop of the global temperatures characterized the late Pliocene, with seasonality and glacial activities increasing in the Northern Hemisphere (Flesche Kleiven et al., 2002). From this, the beginning of the Quaternary (around 2.6 Ma) corresponds to the initiation of the glacial/interglacial cycles marked by a 41 ka periodicity (Zubakov and Borzenkova, 1990, Lourens et al., 1996, Lisiecki and Raymo, 2005). These alternations exacerbated the climatic conditions with successive drop in temperature and humidity from the Gelasian (Kahlke et al., 2011; Head and Gibbard, 2015). In the Italian Peninsula, several cold and arid phases led to a type of vegetation (such as herbaceous plants and shrubs; mostly *Artemisia* and *Ephedra*) typical of open landscapes, while deciduous forests were developed during the more humid interglacial phases with a steady decline of subtropical taxa (Bertini, 2003; Fortelius et al., 2006, Kahlke et al., 2011; Bertini, 2013; Combourieu-Nebout et al. 2015).

Landscape alteration deeply influences mammal communities both in terms of composition (e.g., diversity) and ecology, having to develop new resource exploitation strategies to avoid extinction. This is especially true for large herbivores that, while having the ability to tolerate a range of unfavourable climate oscillations and palaeoenvironmental changes (e.g., from open landscapes to forests, from forests to wooded

steppes), are highly susceptible to vegetation modification and their diets mirror the availability of plant resources (DeMiguel et al., 2010, 2011). By investigating the feeding behaviour of large herbivores, it is thus possible to collect valuable information on how they adapted to, and cope with, alterations in habitat (Fortelius and Solounias, 2000; Solounias and Semprebon, 2002; Rivals and Athanassiou, 2008; Pushkina et al., 2014; DeMiguel, 2016; Bernor et al., 2017, Rivals et al., 2018).

According to the original definition of Azzaroli (1977), the Olivola Faunal Unit (FU) is the first one of the late Villafranchian placed at Gelasian/Calabrian boundary (at 1.8 Ma) (Torre et al., 1992) (Fig. 1A). As a result, this FU records the important changes in the large mammal faunal composition and diversity that occurred at the Gelasian/Calabrian transition and the passage from the middle to the late Villafranchian: the spread of large ungulates living in herds such as the leptobovine *Leptobos etruscus*, of two derived deer (*Eucladoceros dicranios* and *Pseudodama nestii*) and the appearance of the rare Caprinae *Procamptoceras brivatense* whose presence is registered only in the Olivola FU (Gliozzi et al., 1997; Rook and Martinez-Navarro, 2010). Among the carnivores, the first occurrence of the large hyena, *Pachycrocuta brevirostris* and the modern dog, *Canis etruscus* marks the spread of pack-hunter carnivores known as the "Wolf-event" (Azzaroli, 1983) or the "*Pachycrocuta brevirostris* event" due to the high-impact of this carrion eater on the early Pleistocene faunal assemblages (Sardella and Palombo, 2007; Palombo et al., 2008; Martinez-Navarro, 2010). Moreover, the early late Villafranchian also marks the arrival of the first *Homo* populations in the European continent, as testified by the exceptional hominid findings at Dmanisi (Georgia) (Gabunia et al., 1995; Lordkipanidze et al., 2006 and references therein). The Olivola local fauna from northwest Tuscany (Aulla) is the most important site of the Olivola FU and, according to biochronological comparison with the nearby palaeomagnetically calibrated Matassino site, is probably located at the Olduvai Subchron (Gliozzi et al., 1997). Olivola faunal assemblage thus represents an excellent case study to investigate the effects of palaeoenvironmental alterations on large herbivores. By studying the dietary adaptations of the fossil ungulates of this site and by comparing the results with those obtained from the similar faunal assemblage of the middle Villafranchian locality of Coste San Giacomo (Anagni, Central Italy) (Strani et al., 2015, 2017), pivotal information can be gathered on the response of large ungulates in terms of resource exploitation to the climatic changes that occurred during the Gelasian/Calabrian transition.

2. Material and methods

The rich fossil fauna of Olivola comes from fluvial pelitic sandstone and conglomerate deposit ("Olivola Conglomerates") underlying the Olivola village (Aulla, Tuscany) (Fig. 1B). The site is known from the 18th century and palaeontologists as Igino Cocchi and Giovanni Capellini, collected some specimens now stored in the palaeontological museums of the Universities of Pisa and Bologna. At the end of the 18th century the Olivola site was excavated by Forsyth Major (Forsyth Major, 1890) obtaining a large mammal collection now housed at the Natural History Museum of the University of Florence with some fossils stored in the Natural History Museum of London. The site yielded several ungulate remains belonging to 7 taxa: a large bush antlered (*Eucladoceros dicranios olivolanus*) and a medium-sized (*Pseudodama nestii*) deer, a leptobovine (*Leptobos etruscus*), two caprines (*Gallogoral meneghinii* and *Procamptoceras cf. brivatense*), one rhinoceros (*Stephanorhinus etruscus*) and one equid (*Equus stenonis*) (Azzaroli 1950; Napoleone et al., 2003). The material studied consists of 84 teeth belonging to 84 individuals housed at the Natural History Museum of the University of Florence (Florence, Italy).

2.1 Hypsodonty index

Molar crown height (hypsodonty) has been examined as it yields some information about both feeding ecology and habitat openness (especially aridity degree) (Janis, 1988). Crown height in fossil taxa has been measured according to the index defined by Janis (1988) and a Hypsodonty Index (HI) was determined for both unworn (or if not available minimally worn) lower third molars (HIm3) and either upper or lower second molars (HIMm2). The former was determined as m3 height divided by m3 width according to Janis (1988), and teeth classified as brachydont ($HIm3 < 1.5$), mesodont ($1.5 < HIm3 < 2.5$) and hypsodont ($HIm3 > 2.5$). We then calculated an average HIm3 ($n = 5$) for 3 taxa. The latter was determined as the ratio of height to length for unworn either upper or lower second molars (HIMm2) ($n = 11$) following Fortelius et al. (2002) and teeth classified as brachydont ($HIMm2 < 0.8$), mesodont ($0.8 < HIMm2 < 1.2$), and hypsodont ($HIMm2 > 1.2$). An average HIMm2 was also calculated for 4 taxa.

2.2 Dental mesowear

Mesowear is considered a good dietary indicator in herbivore species, as it represents the cumulative effects of the items ingested (both foods and exogenous particles such as dust and grit) on the dental morphology that are produced in a long period of time compared to the lifespan of the animal (Fortelius and Solounias, 2000).

Traditional mesowear (Fortelius and Solounias, 2000), referred as “outer mesowear” (Solounias et al., 2014; Danowitz et al., 2016), analyses the sharpness (i.e., morphology) of the cusps and the height of the occlusal relief of the most labial enamel bands of upper molars and the most lingual of the lower ones (Kaiser and Solounias, 2003; DeMiguel et al., 2012). Occlusal relief (high or low) and cusp shape (sharp, rounded, or blunt) of the apex of the paracone and metacone of upper molars (M1-M3) and the metaconid and entoconid of lower molars (m1-m3) were examined and scored. In the case of the lower molars of the equid *E. stenorhinus* the protoconid and hypoconid were scored (following Kaiser and Fortelius, 2003). Only upper molars (particularly M1 and M2) of *S. etruscus* were analysed as the effect of attrition and abrasion produce different kind of morphologies in rhinoceros lower teeth (Hernesniemi et al., 2011a, 2011b) making comparison with other ungulates mesowear results complex. In all cases, if available, M2 and m2 were preferably selected. The obtained data was then compared with those of a database of extant ungulates with known diets (Fortelius and Solounias, 2000). Occlusal relief and cusp shape scores were also converted to a single mesowear score (MWS) following “mesowear ruler” introduced by Muhlbachler et al. (2011). The method is based on seven cusp types (numbered from 0 to 6), ranging in shape from high and sharp (stage 0) to completely blunt with no relief (stage 6). A total of 80 specimens were scored using this method.

The inner mesowear method, recently developed by Solounias et al. (2014), analyses instead the second enamel band that forms the lingual margin of the metacone or paracone from an occlusal view, which is generally more frequently preserved in fossil specimens. Inner mesowear reflects dietary preferences that are intermediate in time (days-weeks; Solounias et al. 2014; Danowitz et al., 2016) between outer mesowear (months-years; Fortelius and Solounias, 2000) and dental microwear (days-hours; Solounias and Semprebon, 2002). For inner mesowear, the enamel band is scored on the mesial and distal sides of the metacone using a 4 point scaling system described by Solounias et al. (2014) and Danowitz et al. (2016): (1) flat and planar with no gouges or indentations on the surface of the enamel; (2) nearly flat with several gouges that traverse the surface from either edge—the labial and lingual edges of the enamel band are somewhat rounded; (3)

similar to score 2, but more rounded with less defined edges and more gouges; and (4) rounded—the surface is smooth without gouges, and there are no well-defined edges. The junction of the mesial and distal sides termed J is similarly scored: (1) it joins at a sharp, well-defined junction; (2) it is somewhat sharp, and often contains a gouge; (3) it is rounded, but the mesial and distal sides appear as distinct, separate surfaces; and (4) the J point lacks a discrete apex, and the mesial and distal sides of the enamel band form one continuous surface. The method was originally applied by Solounias et al. (2014) only on upper second molars (M2), and here it has been extended to M1 and M3 molars of different individuals (following Strani et al., 2017, 2018) to widen the sample and allow for more complete comparisons among mesowear databases (Table 2). Whenever possible, we used the enamel band of the metacone of the upper molars. If this region was taphonomically damaged, the band of the paracone was examined. We compared our results of the average inner mesowear scores of the mesial, J point and distal surfaces with those of a comprehensive database (Danowitz et al., 2016) of 8 extant ungulates with well-studied diets (browsing, mixed feeding and grazing). A total of 41 specimens were examined using this method.

The obtained mesowear scores were then compared to those of the ungulate taxa of the middle Villafranchian site of Coste San Giacomo previously published in Strani et al. (2015, 2017), which has a similar faunal composition (Bellucci et al., 2012, 2014).

2.3 Statistical analysis

We use hierarchical cluster analysis to distinguish herbivorous taxa groups based on dental wear patterns with percentage of high relief, rounded and blunt cusps of fossil and extant species (data from Fortelius and Solounias, 2000) as variables. The analysis was executed using Euclidean distance and Ward's method. We incorporated also to the study discriminant analyses to examine the resolution of outer mesowear variables applied to the fossil taxa. The percentage of high relief, rounded and blunt cusps were used as independent variables and two dietary (conservative and radical) classifications were used as grouping variables (Fortelius and Solounias, 2000). All analyses were performed using SPSS Statistics 24.

3. Results

3.1 Hypsodonty inference

The deer *E. d. olivolanus* display generally low molar crowns (Table 1) and has a brachydont dentition according to its HI for the lower third molar ($HIm3 = 1.3$) and a mesodont one for the upper or lower second molars ($HIMm2 = 0.8$). The other cervid of the assemblage, *P. nestii*, displays higher crowns and exhibits a mesodont dentition according to both indices ($HIm3 = 1.6$; $HIMm2 = 0.8$). The bovid *L. etruscus* also displays mesodont teeth ($HIMm2 = 1.0$) and *S. etruscus* has brachydont ones ($HIm3 = 0.9$; $HIMm2 = 0.7$) (Table 1). No HI was calculated for *E. stenorhis* because all the dental specimens are either enclosed in the mandible/maxilla or are worn. Nonetheless, this equid is characterized by a highly hypsodont dentition, and HI have been reported for this species and other early Pleistocene equids in other localities (Rivals and Athanassiou, 2008; Strani et al., 2015).

3.2 Dental mesowear

3.2.1 Outer mesowear

The predominant mesowear pattern for the cervids *E. d. olivolanus* and *P. nestii* is to display high occlusal relief and both sharp and rounded cusps with the former having more rounded apices (61.1%) and the latter showing an equal percentage of sharp and rounded cusps (50%). The lack of incidence of blunt cusps for both cervids and the small percentage of low relief observed in *P. nestii* (2.8%) indicate low abrasive diets for these two taxa. The bovids *L. etruscus* and *P. cf. brivatense* show a predominance of high relief (100%) and rounded cusps (100%), which is indicative of intermediate levels of abrasion. The caprine *G. meneghinii* displays equal percentage of high and low occlusal relief and rounded cusps, which point to a slightly more abrasive diet. Among the perissodactyls, *E. stenorhis* exhibits a mesowear comprised of a high percentage of low relief (100%) and blunt apices (60%) (this is the only taxon of the assemblage with this pattern), thereby suggesting a diet with a high degree of abrasion. *S. etruscus* individuals have all high relief (100%) and with mostly rounded cusps (66.7%), indicating relatively low level of abrasion. Olivola fossil ungulates display outer mesowear scores that range from 1.1 (*P. nestii*) to 5.2 (*E. stenorhis*) (Table 2). Cervids have score values comparable to those of modern herbivores with a low or intermediate degree of abrasion in their diets (Fig. 2 A, B, D). Bovids and the rhinocerotids *S. etruscus* display outer mesowear score values comprised between 1.7 (*S. etruscus*) and 3.0 (*G. meneghinii*), which are similar to those of

extant ungulates with an intermediate-to-high abrasive feeding behaviour (Fig. 2 A, B, D). The equid *E. stenorhis* has a score value (5.2) that is close to those of modern grazing herbivores (Fig. 2 A, B, D).

Two main clusters can be observed which separate ungulates with a low-to-medium abrasive diet (cluster A)—composed by browsers (subcluster A.1) and mixed feeders (subcluster A.2)—from those with a highly abrasive feeding (cluster B)—typical of grazers (Fig. 3). *E. stenorhis* falls in the grazer cluster grouped with other extant equids such as *Equus burchellii* and *Equus grevyi*, and with the bovid *Bison bison* (cluster B). *G. meneghinii* is grouped in the grazer cluster as well. *L. etruscus* and *P. cf. brivatense* are both grouped within the mixed feeder cluster with large- and medium sized bovids showing heterogeneous diets (the browser *Tragelaphus strapticerus*, the mixed feeders *Syncerus caffer* and *Redunca redunca*, and the grazers *Kobus ellipsiprymnus* and *Hippotragus equinus*) (subcluster A.2.1). *S. etruscus* also falls into this group close to modern mixed feeders such as *Camelus dromedarius* and *Ovibos moschatus*, among others. Both *E. d. olivolanus* and *P. nestii* are grouped in the mixed feeder cluster with the latter being close to the cervid *Cervus canadensis* (subcluster A.2.2). None of the Olivola fossils fall in the browser cluster.

Discriminant analysis performed with the outer mesowear variables provides a satisfactory dietary discrimination with 74.1% of extant taxa (68.5% in cross-validation) correctly classified according to a conservative classification and 74.1% (74.1% in cross-validation) according to the radical one. The cervids *E. d. olivolanus* and *P. nestii* and the rhinoceros *S. etruscus* are classified as mixed feeders in both the conservative and radical classification (Fig. 4A – B). *L. etruscus* and *P. cf. brivatense* are mixed feeders according to the conservative classification (Fig. 4A), but grazers according to the radical one (Fig. 4B), thereby suggesting a more abrasive, grass-dominated mixed feeding diet for these taxa. *G. meneghinii* and *E. stenorhis* are classified as grazers in both conservative and radical classification (Fig. 4A – B). In both classifications no fossil browsers can be observed.

3.2.2 Inner mesowear

The distribution of the inner mesowear scores (mesial, J point and distal) of the ungulate community of Olivola mostly includes values ≥ 2.0 (Table 2) with the only exception of *P. nestii* which shows scores that ranges from 1.5 to 1.9. *Leptobos* sp., *G. meneghinii* and *E. stenorhis* display the highest values, with the equid having the highest scores (≥ 3.5 in all the three variables). When the inner mesowear scores are plotted

with those of extant ungulates (Fig. 5A), data distribution suggests a dietary diversity comprised by mostly mixed-feeding and grazing traits. *P. nestii* scores are close to those of the modern ungulates *Okapia johnstoni*, *Giraffa camelopardalis* (browsers) and *Cervus canadensis* (mixed feeder), with values that range from 1.3 to 1.8 (data from Solounias et al., 2014). Higher scores are observed in the other cervid *E. d. olivolanus* with values ranging from 2.1 to 2.3 and being close to those of the modern mixed feeder *G. granti*, which displays values from 2.3 to 2.8 (data from Solounias et al., 2014). *L. etruscus* has scores with values (2.6 to 3.1) that are comparable to those of the modern mixed feeder *N. granti* and the modern grazer *Kobus ellipsiprymnus* (3.2 to 3.6; data from Solounias et al., 2014). Both *G. meneghinii* and *E. stenonis* have scores (2.5 to 4.0 for the bovid and 3.3 to 3.7 for the equid) that are comparable to those of modern grazers *Kobus ellipsiprymnus* and *Connochaetes taurinus* (3.2 to 3.9; data from Solounias et al., 2014) and grass dominated-mixed feeder *Ourebia ourebi* (3.6 to 3.8) (Fortelius and Solounias, 2000; Solounias et al., 2014).

3.3 Comparison with the ungulate community of Coste San Giacomo

When mesowear scores of ungulates from Olivola are compared to those from CSG, late Villafranchian taxa display overall higher outer and inner mesowear values (Fig. 2; Fig. 5). When outer mesowear scores are compared (Fig. 2 A–D), Olivola cervids display MWS close to 1.0 (1.2 for *E. d. olivolanus* and of 1.1 for *P. nestii*) whereas the same group in CSG shows very low values, below 0.5 (Table 2), indicating a diet based on the consumption of softer food in this locality. Similarly, bovids from Olivola display a generally higher degree of abrasion in their diet with MWS values comprised between 2 (*Leptobos etruscus*, *P. cf. brivatense*) and 3 (*G. meneghinii*), while their scores range in CSG from 0.2 (*G. torticornis*) to 2 (*Leptobos* sp.). The case of *G. meneghinii* is worth noting, since it is recorded in both sites. According to our results, it displays a mesowear score of 3.0 and 1.0 in Olivola and CSG, respectively. Such clear difference in its mesowear seems to indicate that this species could have successfully fed on a variety of resource types depending on their availability (i.e., seasonally). However, this information should be taken as tentative, as *G. meneghinii* is represented in both Olivola and in CSG by very few (< 5) individuals. The leptobovines have the same outer mesowear scores (2.0) in both localities, while *E. stenonis* has in Olivola a MWS of 5.2 (the highest recorded in this locality), and *E. senegensis* aff. *E. sen. stehlini* (referred as *E. stenonis* in Strani et al., 2017 and in works prior to Palombo et al., 2017) a MWS of 4.7 in CSG. Mean inner

mesowear trends display similar discrepancies between the diets of the Olivola and CSG taxa (Fig. 5A, B). Olivola inner mesowear score values are mostly above 2 with three species (*L. etruscus*, *G. meneghinii* and *E. stenonis*) displaying very high values (ranging from 2 to 4) (Fig. 5A) while most of the taxa in CSG display low or intermediate inner mesowear (from 1 to 3) scores, with only one species (*E. senezensis* aff. *E. sen. stehlini*) having values above 3, and with *G. meneghinii* having much lower values than in Olivola (Fig. 5B). The medium-small deer *P. nestii* from Olivola and *A. cf. lyra* from CSG show, however, similar inner mesowear low values, around 1.5 (Fig. 5A, B).

4. Discussion

Hypsodonty is mostly associated to wear resistance with higher crowns indicating a higher level of abrasion in dry and open habitats (e.g. grasslands) (Janis, 1988; Eronen et al., 2010a; 2010b), though it appears to be also linked to biomechanical effectiveness on consuming resistant items (DeMiguel et al., 2015). Considering these factors, the presence of one hypsodont, two mesodont, one brachydont and one brachy-mesodont ungulate seems to suggest a certain degree of aridity and habitat openness. When the dental wear patterns are taken into account, the absence of strict browsers suggests that soft, ligneous plant resources were not abundant in the region, while the occurrence of two strict grazers (*G. meneghinii* and *E. stenonis*) and of mixed feeders with a strong tendency towards grazing (*L. etruscus* and *P. cf. brivatense*) indicates diffused open and dry grasslands. The presence of ungulates with a mixed feeding behaviour (*E. d. olivolanus* and *S. etruscus*) and of a mixed feeder with a diet richer in browse (*P. nestii*) on the other hand points out to incidence of less opened areas possibly represented by patchy thickets or open woodlands.

This setting differs from that recently reconstructed (Strani et al., 2015, 2017) for the middle Villafranchian (Gelasian) site of CSG, where a mosaic of habitats, from wetlands to closed forests to grasslands, was inferred based on hypsodonty and dental mesowear of the ungulate taxa. In strong contrast to the ungulate community of Olivola, the CSG herbivores display diversified dietary adaptations (Table 3) with several browsers (*Axis cf. lyra*, *Croizetoceros cf. ramosus*, *Eucladoceros* sp., *Gazellospira torticornis*) and mixed feeders (*Gazella borbonica*, *Gallogoral meneghinii*, *Leptobos* sp.), and a strict grazing feeding behaviour represented by the equid *E. senezensis* aff. *E. sen. stehlini*.

In the Italian Peninsula, palynological data from the Poggio Rosso section (Montevarchi Synthem Depositional Unit) from the geographically close Upper Valdarno Basin (Tuscany, Central Italy), reveal a significant increase (up to 89%) in herbs, mostly Asteraceae and Cichorioideae, before the top of the Olduvai subchron marking a cold and dry phase possibly corresponding to the MIS 64 (Bertini et al., 2010; Bertini, 2013). In the same section, in deposits between 2.2 and 1.7 Ma, a general decrease of plant species diversity is recorded and a loss of subtropical taxa is attested (Bertini, 2013), a trend that characterizes the whole vegetation of the Italian Peninsula at the beginning of the Pleistocene (Bertini, 2003; Bellucci et al., 2014; Combourieu-Nebout et al., 2015).

According to all these data, it is possible to increase our understanding about how large herbivores adapted to the overall direction towards colder and drier conditions of the early Pleistocene in the Italian Peninsula. First, our data show that bovids and cervids most prominently shifted their feeding behaviours towards a diet richer in abrasive plants, thereby taking advantage of the expansion of herbaceous and steppe vegetation (Bertini, 2003, 2013) (Table 2). Considering the different degree of hypsodonty observed in these groups, bovids may have fed on plants with abundant phytolith production (e.g. grasses) while brachy- or mesodont deer on herbs with a lower silica content (e.g. forbs) (Piperno, 1988, 2006; Morris et al., 2009). This shift towards a more abrasive diet is particularly evident in the fossil deer: the large sized bush-antlered deer *Eucladoceros* and the medium-to-small sized deer (*Pseudodama nestii*, *Axis* cf. *lyra*) which clearly adopted a strict browsing behaviour in CSG, display a mixed diet in the more recent site of Olivola. Few studies are available on the diet of medium or small sized middle/early late Villafranchian fossil deer (such as *Pseudodama* and *Croizetoceros*), but in other similarly dated localities in Europe (e.g., Greece, France and Britain), these taxa usually display a browsing or mixed feeding behaviour (Rivals and Athanassiou, 2008; Valli and Palombo, 2008; Rivals and Lister, 2016a). Contrary a recent study based on the dental microwear texture analysis reported a greater diversity of feeding behaviours (from browser to grazer) for the large bush-antlered deer *E. ctenoides*, suggesting a significant dietary plasticity for this early Pleistocene cervid (Berlioz et al., 2017). Dental microwear however records information about the last few meals (hours and days) of an animal before its death (whereas dental mesowear reflects dietary preferences over a longer period; weeks and months) (Sánchez-Hernández et al., 2016; Mithlacher et al. 2018), thus the observed discrepancy could reflect seasonal differences. A more abrasive diet is also recorded for the Olivola

specimens of *E. d. olivolanus* (mixed feeder) and for *P. nestii* (browse-dominated mixed feeder), suggesting that in the Italian Peninsula, both *Eucladoceros* lineage and the "Axis-like" deer group (which include fossil *Axis*, *Pseudodama* and *Metacervoceros*), adapted to exploit a wider spectrum of food resources during the late Villafranchian, probably driven by the steady reduction of subtropical-like environments, especially during glacial periods (Bertini et al., 2010; Combourieu-Nebout et al. 2015). The development of this dietary plasticity may have been a winning strategy for the spread of both groups through the European continent which occurrences are reported up to the Epivillafranchian and early Galerian (Rook and Martinez-Navarro, 2010; Bellucci et al., 2015). The same flexibility in food exploitation is also observable in extant cervids such as the red deer (*Cervus elaphus*) (Gebert and Verheyden-Tixier, 2001), the sika deer (*Cervus nippon*) (Takatsuki, 2009; Kubo et al., 2014) or in the modern chital (*Axis axis*) (Sankar and Acharya, 2004). Dietary flexibility has been also demonstrated in a large variety of extinct herbivorous mammals (including deer, giraffids, dromomerycids, proboscideans, antilocaprids, etc) across their range (Solounias et al., 1988; 2000; Solounias and Moelleken, 1994; Semperebon et al., 2004; Rivals et al., 2009, 2012; DeMiguel et al., 2008, 2010; Kahlke and Kaiser, 2011; Rivals and Semperebon, 2011; Haiduc et al., 2018, Strani et al., 2018), probably as a response to environmental shifts and changing environments (DeMiguel et al., 2010). The leptobovine lineage assumes consistently a grass-dominated mixed feeding behaviour in both localities, whereas *G. meneghinii* displays a more abrasive diet in Olivola than in CSG. *E. stenonis* and *E. senegensis* aff. *E. sen. stehlini* exhibits dental wear patterns that are typical of extant grazer species in both sites, with the equid from Olivola having blunter cusps suggesting a stricter grazing behaviour in this locality. Although no mesowear data of *S. etruscus* from the CSG are available, tooth meso- and microwear data from East Runton (Britain) (Rivals and Lister, 2016a) suggest a browsing behaviour for this species. The mixed diet inferred for this species in Olivola can be considered, therefore, as an adaptation to the drier conditions, which is in well accordance with the case of the remaining cervids.

Overall the mesowear signatures of the cervids *P. nestii* and *E. d. olivolanus* appear to be comparable to that of the modern mixed feeder wapiti (*Cervus canadensis*), a large deer that shows high occlusal reliefs, no blunt cusps, and similar percentages of sharp and rounded cusps (Fortelius and Solounias, 2000). This large deer feeds mostly on shrubs, tree shoots, sedges and grasses in both meadows and forested areas (Mattioli, 2011; Jung et al., 2015). Accordingly, both fossil deer could have exhibited similar dietary

preferences, thus feeding in both open and closed areas and partitioning the available resources through body size differences (*Eucladoceros* is a large deer with a body mass of over 200 kg similar to that of modern red deer; Kaiser and Croitor, 2004; Baygusheva and Titov, 2013; Strani et al., 2017), with *P. nestii* displaying a more selective browsing behaviour. The large *E. stenonis*, *S. etruscus* and *L. etruscus* most probably foraged in grasslands, with the bovid and the rhinocerotid adopting a more generalist diet. *P. cf. brivatense*, a small caprine quite rare and often poorly represented in the fossil record (Crégut-Bonnoure, 2007), may have occupied open areas as well, and exhibited a mixed diet somewhat rich in abrasive items. Alcalde (2013) reports postcranial morphologies typical of ungulate adapted to rocky and steep areas for *G. meneghinii* suggesting that this species in Olivola like in the middle Villafranchian site of CSG may have preferred mountainous habitats. Unlike in CSG, the only individual of *G. meneghinii* suggests a diet based on high consumption of abrasive items (e.g., grasses, dust, and grit), but the small sample available in both localities does not allow for more precise inferences.

Other late Villafranchian European and Western Asian localities, as Barranco de los Conejos (Guadix-Baza Basin, Spain) and Dmanisi (Caucasus, Georgia), have also been object of climatic and palaeoenvironmental reconstructions. In Barranco de los Conejos, a trend towards drier and colder conditions has been documented for the lowermost levels in the upper Matuyama Chron, as indicated by the evolution of the arvicolid local lineages towards developing ever-growing molars, and evidences from other vertebrate assemblages (Agustí et al., 2013). Different proxies (pollen, phytoliths, fossil fruits, herpetofauna, insectivorans, micro- and large mammals) suggest the presence of arid environments at Dmanisi as well, ranging from steppe or semi-desert to open Mediterranean forests in a warm and dry Mediterranean climate (Gabunia et al., 2000; Blain et al., 2014 and references therein).

The Gelasian/Calabrian transition (middle/late Villafranchian) in Southern Europe seems to have been characterized by an increase of the aridity level (though some areas such as Sésiklo in Greece exhibited mostly arid conditions even during the middle Villafranchian, as reported by Rivals and Athanassiou, 2008 or experienced an expansion of steppes restricted in time and space such as in the Padania plain, as reported by Bertini, 2010 and references therein) and in the Italian Peninsula this change seems to have led ungulates, browsers in particular, to adapt to consume more abrasive foods in response to the expansion of grasslands and steppe-like vegetation.

5. Conclusions

Analysis of the dental morphology and mesowear patterns of the Olivola ungulates allowed us to gather new information about the response of fossil ungulates to the Gelasian/Calabrian climatic changes, and on the habitats that characterized the region during this phase of significant environmental modifications. The occurrence of taxa with, mostly, medium-to-high molar crowns coupled with the lack of strict browsers, the abundance of mixed feeders (*E. d. olivolanus*, *P. nestii*, *L. etruscus*, *P. cf. brivatense*, *S. etruscus*) and grazers (*G. meneghinii*, *E. stenonis*) reflects a mostly dry landscape characterized by open grasslands with subordinate thickets and open woodlands. Overall when compared to the middle Villafranchian (Gelasian) fossil ungulate assemblage of Coste San Giacomo, the late Villafranchian herbivores of Olivola display less diversified dietary behaviours. Cervids and *G. meneghinii* shifted to a more abrasive diet exploiting the now more open landscapes, suggesting a high dietary plasticity for these groups.

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Figure captions

Figure 1: A, Integrate chronological scheme for the Fontana Ranuccio Faunal Unit (modified from Gliozzi et al., 1997); B, geographical location of the early Pleistocene sites of Olivola and Coste San Giacomo.

Figure 2: Outer mesowear results of fossil (from Olivola and Coste San Giacomo, CSG) and extant ungulates. CSG data converted from Strani et al. (2015); modern ungulates data from Fortelius and Solounias (2000) and Rivals et al. (2010, 2014, 2016b). A, Mean mesowear score (MWS) of fossil families from Olivola; B, mean MWS of single taxa from Olivola; C, mean MWS of fossil families from CSG; D, mean MWS of single taxa from CSG; E, extant ungulates and dietary categories. Fossil taxa abbreviations: Al, *Axis*

cf. *lyra*; Cr, *Croizetoceros* cf. *ramosus*; Ed, *Eucladoceros dicranios olivolanus*; Es, *Equus stenonis*; Ez, *E. senezensis* aff. *E. sen. stehlini*; Eu, *Eucladoceros* sp.; Gb, *Gazella borbonica*; Gt, *Gazellospira torticornis*; Gm, *Gallogoral meneghini*; Pn, *Pseudodama nestii*; Le, *Leptobos etruscus*; Lp, *Leptobos* sp.; Pb, *Procamptoceras* cf. *brivatense*; Se, *Stephanorhinus etruscus*. Other abbreviations: FB, extant fruit browsers; LB, extant leaf browsers; M, extant mixed feeders; G, extant grazers. Error bars correspond to standard deviation (± 1 SD).

Figure 3: Mesowear hierarchical cluster diagram based on the percentage of high occlusal relief, round and blunt cusps of fossil populations with extant species (data for extant species from Fortelius and Solounias, 2000).

Figure 4: Bivariate diagrams based on discriminant analysis: A, conservative classification; B, radical classification. Fossil taxa abbreviations: Ed, *Eucladoceros dicranios olivolanus*, Pn, *Pseudodama nestii*; Le, *Leptobos etruscus*; Gm, *Gallogoral meneghini*; Pb, *Procamptoceras* cf. *brivatense*; Es, *Equus stenonis*; Se, *Stephanorhinus etruscus*.

Figure 5: Comparison between inner mesowear scores of fossil ungulates from Olivola and CSG. A, Mean inner mesowear scores for Olivola fossil taxa and modern browsers, mixed feeders and grazers (data for extant species from Danowitz et al., 2016); B, mean inner mesowear scores for CSG fossil taxa (data from Strani et al., 2017) and modern browsers, mixed feeders and grazers (data for extant species from Danowitz et al., 2016). Fossil taxa abbreviations: Al, *Axis* cf. *lyra*; Cr, *Croizetoceros* cf. *ramosus*; Ed, *Eucladoceros dicranios olivolanus*; Es, *Equus stenonis*; Ez, *E. senezensis* aff. *E. sen. stehlini*; Eu, *Eucladoceros* sp.; Gb, *Gazella borbonica*; Gt, *Gazellospira torticornis*; Gm, *Gallogoral meneghini*; Pn, *Pseudodama nestii*; Le, *Leptobos etruscus*; Lp, *Leptobos* sp.; Pb, *Procamptoceras* cf. *brivatense*; Se, *Stephanorhinus etruscus*. Other abbreviations: B, modern browsers; M, modern mixed feeders; G, modern grazers.

Table captions

Table 1. Summary of hypsodonty results. Abbreviations: Number of specimens measured (N); hypsodonty index calculated as in Janis (1988) (HIm3); hypsodonty index calculated as in Fortelius et al. (2002) (HIMm2)

Table 2. Summary of outer and inner mesowear. Abbreviations: Number of specimens (N); percentage of specimens with high (%High) and low (%Low) occlusal relief; percentage of specimens with sharp (PerSharp), rounded (PerRound) and blunt (PerBlunt) cusps; outer mesowear score (MWS); mesial (Mesial), distal (Distal) and J point (J) scores. CSG outer mesowear scores from Strani et al. (2015) with the 4 points method proposed by Rivals et al. (2007) converted to the 7 points method proposed by Muhlbachler et al. (2011).

Table 3. Summary table of dietary behaviours of the ungulates of Olivola and CSG (CSG data from Strani et al., 2015, 2017)

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Table 1

Taxa	Hypsodonty Index							
	N	HIm 3	HIm3 min/max	Category	N	HIMm 2	HIMm2 min/max	Category
<i>Eucladoceros dicranios olivolanus</i>	1	1.3	1.3	brachyodont	3	0.8	0,83/0,86	mesodont
<i>Pseudodama nestii</i>	3	1.6	1,39/1,71	mesodont	6	0.8	0,74/0,86	mesodont
<i>Leptobos etruscus</i>	/	/	/	/	1	1.0	1.0	mesodont
<i>Gallgoral meneghinii</i>	/	/	/	/	/	/	/	/
<i>Procamptoceras cf. brivatense</i>	/	/	/	/	/	/	/	/
<i>Equus stenonis</i>	/	/	/	/	/	/	/	/
<i>Stephanorhinus etruscus</i>	1	0.9	0.9	brachyodont	2	0.7	0,63/0,75	brachyodont

Table 2

Locality	Taxa	Outer Mesowear			PerSharp	PerRound	PerBlunt	MWS	Inner Mesowear			J
		N	%High	%Low					N	Mesial	Distal	
OLIVOLA												
	<i>Eucladoceros dicranios olivolanus</i>	18	100	0	38.9	61.1	0	1.2	10	2.1	2.1	2.3
	<i>Pseudodama nestii</i>	36	97	2.8	50	50	0	1.1	18	1.5	1.5	1.9
	<i>Leptobos etruscus</i>	14	100	0	0	100	0	2.0	8	3	3.3	3.3
	<i>Gallgoral meneghinii</i>	2	50	50	0	100	0	3.0	2	2.5	4	3
	<i>Procamptoceras cf. brivatense</i>	2	100	0	0	100	0	2.0	/	/	/	/
	<i>Equus stenonis</i>	5	0	100	0	40	60	5.2	3	3.7	3.7	3.3
	<i>Stephanorhinus etruscus</i>	3	100	0	33.3	66.7	0	1.7	/	/	/	/
COSTE SAN GIACOMO												
	<i>Axis cf. lyra</i>	26	100	0	76.9	23.1	0	0.4	7	1.5	1.8	1.4
	<i>Croizetoceros cf. ramosus</i>	5	100	0	80	20	0	0.4	3	1.0	1.5	1.7
	<i>Eucladoceros</i> sp.	26	100	0	88.5	11.5	0	0.2	12	1.3	1.5	1.8
	<i>Gazella borbonica</i>	8	87.5	12.5	50	50	0	1.3	2	2.5	2.5	3.0
	<i>Gazellospira torticornis</i>	8	100	0	87.5	12.5	0	0.3	4	1.5	1.0	1.8
	<i>Gallgoral meneghinii</i>	2	100	0	50	50	0	1.0	2	1.5	1.0	2.0
	<i>Leptobos</i> sp.	2	100	0	0	100	0	2.0	2	2.5	2.5	2.5
	<i>E. senezensis</i> aff. <i>E. sen. stehlini</i>	21	4.8	95.2	28.6	38.1	28.6	4.7	11	3.3	3.3	3.6

Table 3

	Dietary behaviour	
Group	Olivola	CSG
Cervids	mixed feeders/browse-dominated mixed feeders	strict browsers
Bovids		
antilopines	–	browser/mixed feeders
caprines	grass-dominated mixed feeders/grazers	mixed feeders
leptobovines	grass-dominated mixed feeders	grass-dominated mixed feeders
Rhinocerotids	mixed feeders	–
Equids	grazers	grazers

Highlights

- The paleoecology of the Olivola mammal fauna is investigated
- Narrow range of ungulate diet types at the Gelasian/Calabrian transition
- New data on the diet of rare Pleistocene bovids provided by dental mesowear

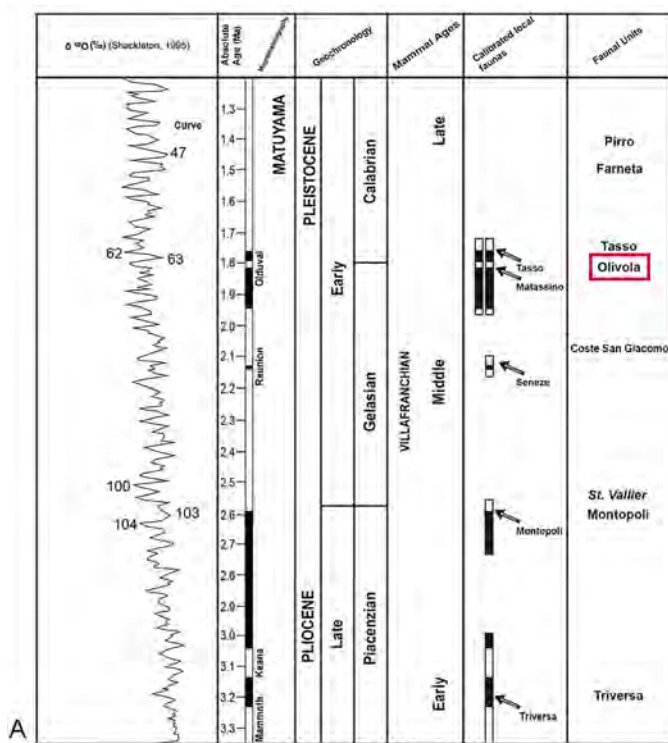


Figure 1

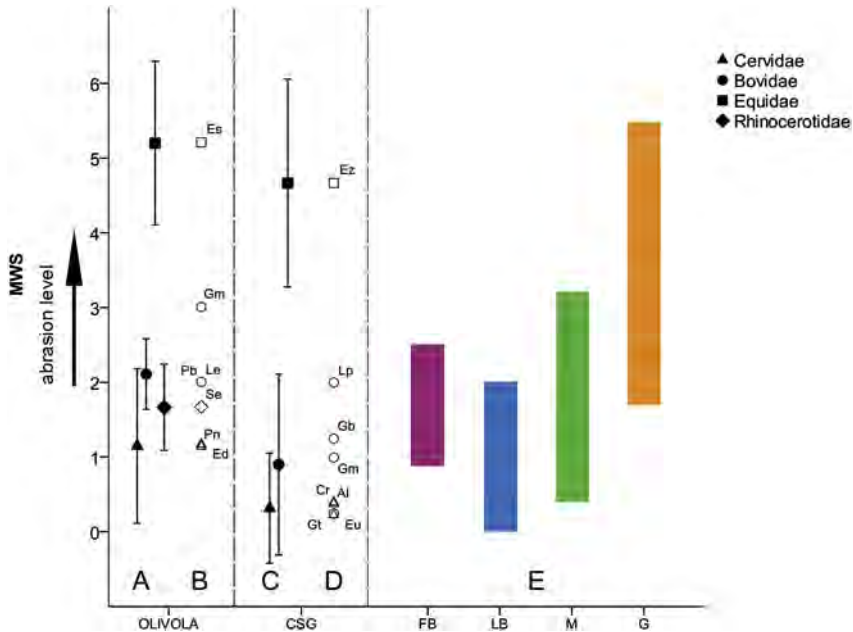


Figure 2

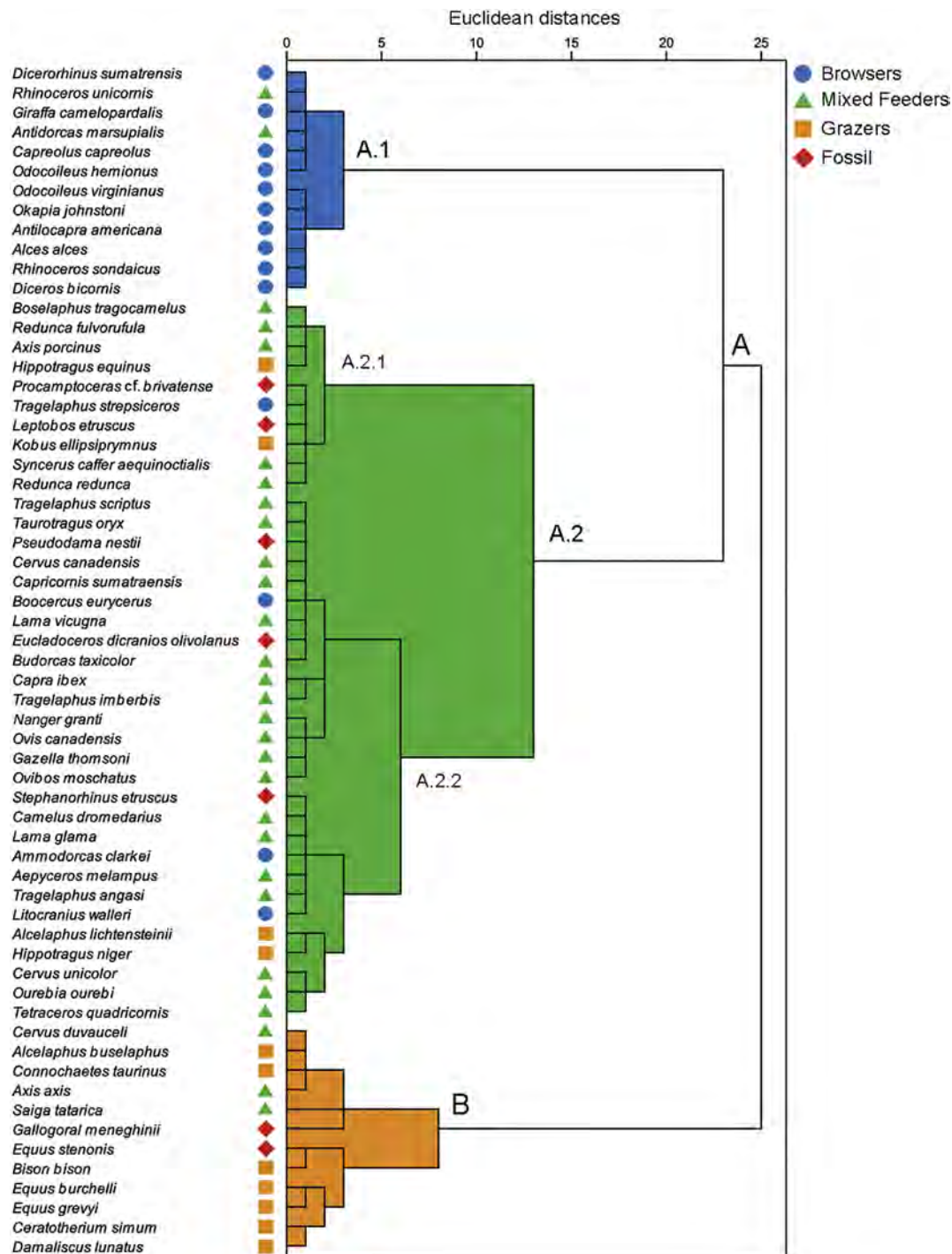
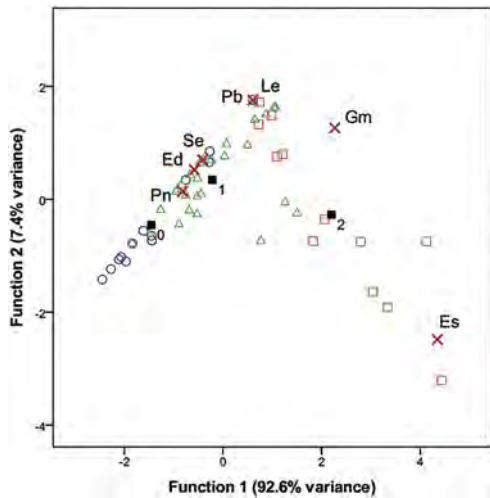
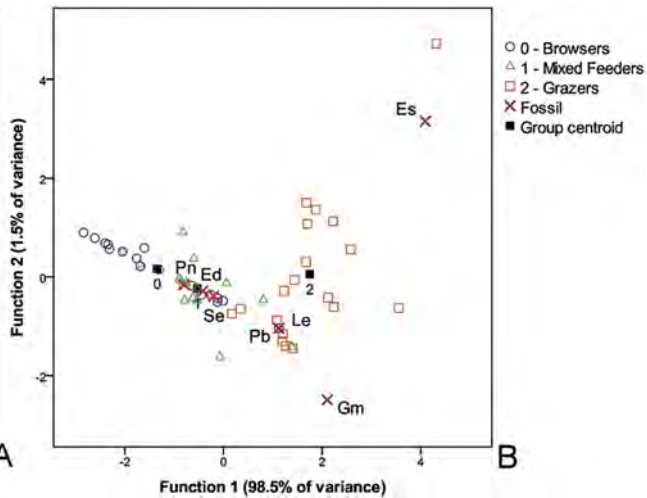


Figure 3



A



B

Figure 4

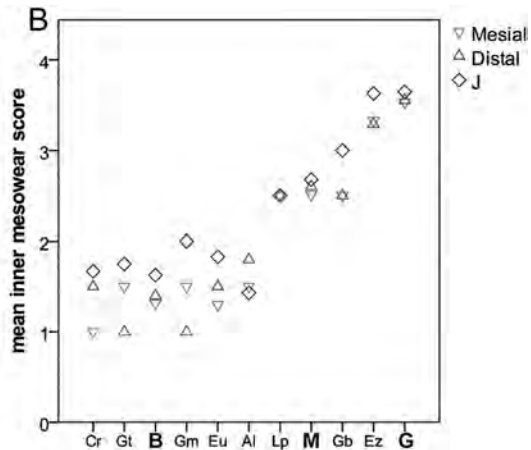
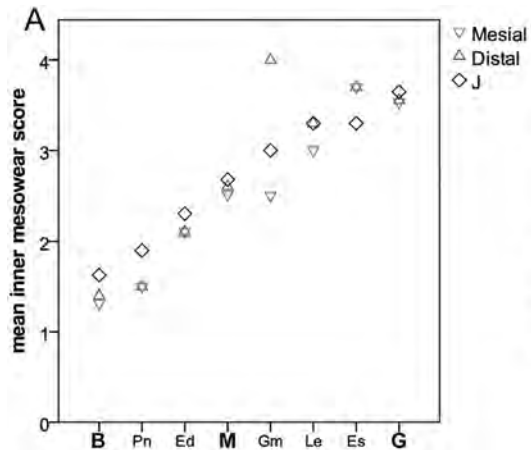


Figure 5